

**A NEW SPECIES OF *OPHRAELLA* WILCOX  
(COLEOPTERA: CHRYSOMELIDAE) FROM THE  
SOUTHEASTERN UNITED STATES**

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*Abstract.*—*Ophraella slobodkini*, new species, is described from the southeastern United States. It shares the host association of *Ambrosia artemisiifolia* with *O. communa* LeSage, but is a sibling species of *O. notulata* Fabricius. The three species can be statistically distinguished using morphological characters, and reliably distinguished by electrophoretic mobility of several enzymes.

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*Ophraella* (Wilcox, 1965) is a North American genus of leaf beetles (Chrysomelidae: Galerucinae, Galerucini), the species of which are specifically associated with various Asteraceae (Compositae). Among the currently recognized species (LeSage, 1986, Futuyma, 1990), one is associated with *Iva frutescens* (marsh elder) along the Atlantic and Gulf coasts, and another is associated with *Ambrosia artemisiifolia* (common ragweed) throughout much of North America. LeSage (1986) applied the name *notulata* Fabricius to the *Iva*-associated species, which had hitherto been referred to *integra* LeConte, and designated as *Ophraella communa* LeSage the *Ambrosia*-associated species, which prior to LeSage's work had borne the epithet *notulata*. In the course of a study of the evolution of host associations in *Ophraella* (Futuyma, 1990; Futuyma and McCafferty, 1990), an undescribed species has come to light. Although it shares the host association (*Ambrosia artemisiifolia*) of *O. communa*, it is a sibling species of *O. notulata*, from which it is statistically distinguishable by a few morphological features, and reliably distinguishable by the electrophoretic mobility of several enzymes. In appreciation of my mentor and colleague, the ecologist Lawrence B. Slobodkin, I gratefully designate it

***Ophraella slobodkini*, new species**

*Diagnosis.* Morphologically, this species is indistinguishable from *Ophraella notulata* (Fabricius) except by the following differences which characterize many but not all specimens. The anterior margin of the labrum is slightly concave; in a minority of specimens it is even or slightly convex, the usual condition in *O. notulata*. The pronotum is anteriorly usually glabrous (extending to ca. 10% of the distance from the margin), whereas it is usually fully setiferous in *O. notulata*. In some but not all populations of *O. slobodkini*, crossbars of dark pigment often extend between the subsutural and cubital ("supplementary" of LeSage, 1986) elytral vittae (rarely so in *O. notulata*). Slight differences in shape between these species will be noted below. The only known host of *O. slobodkini* is *Ambrosia artemisiifolia*, whereas *O. notulata* is only known to feed on *Iva frutescens* and *I. annua*.

*Description of imago.* Size: Linear measurements (mean and standard deviation, in mm, measured with ocular micrometer; N = 35 pinned females and 36 males from several locations as listed below): Total length (front of head to apex of elytra, in dorsal view) of females  $4.96 \pm 0.222$ , of males  $4.35 \pm 0.231$ ; length of elytra (base of humerus to apex) of females  $3.95 \pm 0.179$ , of males  $3.45 \pm 0.152$ ; width of pronotum of females  $1.59 \pm 0.058$ , of males  $1.43 \pm 0.057$ ; maximal width of left elytron of females  $1.35 \pm 0.068$ , of males  $1.13 \pm 0.061$ .

Coloration: Ground color yellowish brown (testaceous). Dark brown to black coronal mark, apices of antennomeres and leg segments, labrum (except base), and venter (variably testaceous to piceous). Pronotum with a dark medial macula, a lateral macula, and in some specimens a small macula lateral to the latter. Each elytron with four dark brown to black vittae: lateral vitta extending from base of humerus nearly to apex, joining the subsutural vitta; subsutural vitta extending fully to base or becoming evanescent in basal quarter; discal vitta extending from base to apex, usually approaching or joining the subsutural; cubital (supplementary) vitta extending obliquely toward suture from base to apex, confluent with subsutural vitta at about 70% of the distance from the base and forming a single vitta thereafter; cubital and subsutural vittae frequently joined by dark crossbands at base and more distally, these expanded in some specimens, leaving only small windows between the almost fully confluent vittae. Some specimens with interruptions in discal, cubital, and/or subsutural vittae, and with the discal vitta weak or evanescent basally and apically.

Setation and punctation: Setae of head dense on vertex, sparser on frons and genae; frontal tubercles glabrous, slightly punctate; pronotum dorsally with fairly dense setae except near anterior margin, coarsely punctate, the punctures confluent posteriorly; elytra densely and evenly invested with short, fine, recumbent setae and bearing sparse erect setae, especially posteriorly along vittae; setae of epipleuron sparser; elytral punctures dense, very small, separated by distances equal to or slightly greater than their diameter, slightly larger basally, their pattern not altered in vicinity of vittae.

Other structural features: Pronotum rather flat, explanate rather than arched, broadest at or slightly behind middle, lateral margins evenly convex or almost straight before the middle, anterior margin slightly concave, posterior margin sinuous, medially concave. Posterior margin of scutellum convex. Setae of mouthparts (each side): prementum 1; cardo 1–3 (mode = 1), apicolateral; maxillary palpifer 1 or 2 (mode = 1); labrum with 5 small lateral setae on anterior margin. Mandible lacking visible setae or serrations on margin of teeth. Sternum VIII of female (LeSage, 1986) shallowly emarginate at apex, with a broad stem between the lateral wings and the laterally extended base; mean ratio of stem width to sternum length 0.79 (N = 4), ratio of breadth across wings to length 1.15. Spermatheca narrow throughout, with receptacle and pump hardly inflated; apex of spermathecal pump simple, lacking appendage. Sternum VIII and spermatheca closely resembling condition in *O. notulata* (LeSage, 1986, figs. 72, 78). Male genitalia indistinguishable from *O. notulata* (LeSage, 1986, fig. 69); sexual dimorphism in visible terminal tergum and sternum, and other characters generally, as in other members of the genus (LeSage, 1986).

*Type material.* Holotype, female: Florida, Leon Co., 30°39'30"N, 84°12'30"W, 6.5 km west of Iamonia, at Tall Timbers Research Station, elevation 45 m, Douglas J. Futuyma, collector, 24 April 1989. Paratypes: Nineteen specimens with data as for



the holotype. Holotype (C. U. type number 6505) and paratypes deposited in the Cornell University Insect Collection, Ithaca, New York.

*Other deposited material.* (Unless otherwise noted, all were collected by the author, with assistance from M. Keese.) Georgia, Thomas Co., Thomasville, 24 April 1989 (2 specimens); Florida, Escambia Co., Co. Rd. 293, ca. 19 km W of Pensacola, 22 May 1986 (1); Florida, Duval Co., Lawtey, 20 April 1989 (5); Florida, Flagler Co., Bunnell, 21 April 1989 (15); Florida, Broward Co., Merritt Island National Wildlife Refuge, 21 April 1989 (20); Florida, Pasco Co., Slaughter (in Withlacoochee National Forest), 22 April 1989 (20); Florida, Broward Co., Dania, 24 December 1988 (35), 13 December 1985 (3, coll. D. Furth). All specimens, including type series, collected on *Ambrosia artemisiifolia*. Deposited as follows: Cornell University Insect Collection (Thomasville, Ga., 2; Bunnell, Fla., 10; Slaughter, Fla., 5; Merritt Island NWR, Fla., 10; Lawtey, Fla., 5; Escambia Co., Fla., 1; Dania, Fla., 10), American Museum of Natural History, New York (Merritt Island NWR, 5; Dania, 5), U.S. National Museum, Washington (Slaughter, 5; Dania, 5), Florida State Collection of Arthropods, Gainesville (Merritt Island NWR, 5; Slaughter, 5; Dania, 5), Museum of Comparative Zoology, Harvard University (Bunnell, 5; Dania, 5), Canadian National Collection, Ottawa (Slaughter, 5; Dania, 5). Some specimens are retained by the author at the State University of New York at Stony Brook.

*Morphological and electrophoretic distinctions among Ophraella slobodkini, O. notulata, and O. communa.* The larvae of *O. slobodkini* appear indistinguishable from those of *O. notulata* and *O. communa* in all characters examined, including mouthparts and setation. Larvae of *O. notulata* in the north (New York, New Jersey) have broad, almost coalescent vittae, but in specimens from Florida, the vittae are narrower and do not distinguish this species from *O. slobodkini*. The adults of *O. slobodkini* and *O. notulata* are statistically distinguishable only by the characters noted in the diagnosis and by shape, as noted below. *Ophraella communa*, which also feeds on *Ambrosia artemisiifolia*, is distinguishable from *O. slobodkini* by its pattern of elytral vittae (the cubital vitta is directed more abruptly toward the sub-sutural vitta, and terminates in or near it about halfway from the base), by its broader shape (see below), by its longer, more erect, and more variously oriented elytral setae, by its larger elytral punctures, by the greater number of setae on the cardo ( $\bar{x} = 5.5$ ) and maxillary palpifer ( $\bar{x} = 2$ ), and by the form of the spermatheca and sternum VIII in the female (LeSage, 1986, figs. 101, 107).

Compared to *Ophraella notulata*, in *O. slobodkini* the pronotum and elytra are slightly, although statistically significantly, broader relative to elytron length (Table 1), the hind tibia is relatively longer, and the pronotum is broader relative to the width across the humeri. *Ophraella slobodkini* has relatively narrower elytra than *O. communa*, which lies between *O. slobodkini* and *O. notulata* in the relation of pronotum breadth to elytron length and breadth across the humeri. The slope of most of these relationships, which are nearly isometric within species, does not differ significantly.

To correct for correlations among these several measurements, multivariate analyses were performed (by D. Slice), using all variables in Table 1 except tibia length (because of missing data). Data were entered separately for the sexes (sample sizes for females and males, respectively, were 34, 36 *O. slobodkini*, 18, 21 *O. notulata*, 17, 22 *O. communa*). Each measurement was log<sub>e</sub>-transformed to achieve normal distributions, and was divided by the arithmetic mean of the individual's several

Table 1. Regression equations for pairs of linear measurements (in micrometer units, at 18×) on *Ophraella slobodkini*, *O. notulata*, and *O. communa*. Tests for significant differences between species in slope and in mean values of Y adjusted to common X are based on analyses of covariance (Sokal and Rohlf, 1981). Sample of *O. slobodkini* is of specimens from Iamonia, Bunnell, Slaughter, Merritt Island NWR, and Dania, Florida; of *O. notulata*, from Citrus and Dixie Co., Fla. (7), Bluffton, S.C. (23), and Tuckerton, N.J. (9), of *O. communa*, from Iamonia, Fla. (10), Thomasville, Ga. (11), and Suffolk Co., N.Y. (18). Sex ratios are approximately 1:1 for all species.

Species	N	MS <sub>y·x</sub>	Regression equation	Comparison <sup>1</sup>	Difference between adjusted means		Difference between adjusted slopes	
					F	P	F	P
1. Maximum breadth of elytron (Y) vs. length of elytron (X)								
<i>O. slobodkini</i>	70	0.990	Y = -6.207 + 0.419X	s/n	15.343	0.001	0.151	n.s.
<i>O. notulata</i>	39	1.242	Y = -8.114 + 0.432X					
<i>O. communa</i>	39	0.762	Y = 1.420 + 0.329X	s/c	24.152	0.001	9.020	0.005
2. Breadth of pronotum (Y) vs. length of elytron (X)								
<i>O. slobodkini</i>	70	0.596	Y = 7.823 + 0.304X	s/n	34.537	0.001	1.181	n.s.
<i>O. notulata</i>	39	1.117	Y = 4.284 + 0.336X					
<i>O. communa</i>	39	1.346	Y = 5.495 + 0.343X	s/c	7.953	0.010	1.800	n.s.
3. Breadth of elytron (humerus to suture) (Y) vs. breadth of pronotum (X)								
<i>O. slobodkini</i>	70	0.438	Y = -0.286 + 0.685X	s/n	7.221	0.025	0.945	n.s.
<i>O. notulata</i>	39	0.663	Y = 2.100 + 0.621X					
<i>O. communa</i>	39	0.403	Y = 0.849 + 0.675X	s/c	37.271	0.001	0.037	n.s.
4. Length of hind tibia (Y) vs. length of elytron (X)								
<i>O. slobodkini</i>	66	1.729	Y = 15.357 + 0.280X	s/n	26.571	0.001	4.962	0.050
<i>O. notulata</i>	39	1.479	Y = 6.146 + 0.379X					

<sup>1</sup> Comparisons are among *O. slobodkini* (s) and *O. notulata* (n) or *O. communa* (c).



log-transformed measurements. The latter procedure corrects for differences in size, so that the standardized measurements describe shape. A multivariate analysis of variance (not shown) on the standardized measurements indicated statistically significant differences in shape between sexes and among species (the sex by species interaction was not significant). The shape differences among species and sexes are displayed in Figure 2, which presents the first two canonical variates from a canonical discrimination analysis (using the CANDISC procedure of SAS), in which the within-group variances were standardized to 1.0. The sexes (open vs. closed symbols) are largely discriminated by canonical variate 2, whereas both variates, especially variate 1, discriminate the species. The shape of *O. slobodkini* is intermediate between that of *O. notulata* and *O. communa*, although closer to and overlapping *O. notulata*.

Sibling species are frequently most definitively distinguished by enzyme electrophoresis (Menken, 1989). Several enzymes offer the most diagnostic differences between *Ophraella slobodkini* and *O. notulata*, and provide clear evidence that they are distinct species (Table 2). These species are almost fixed for different alleles at the faster of two isocitrate dehydrogenase loci (IDH2), and the most common allele of glucose phosphate isomerase (GPI) in *O. slobodkini* is absent in *O. notulata*. In addition, allele frequencies differ strongly at the leucine aminopeptidase (LAP) locus. These differences hold for syntopic samples of the two species taken from their respective host plants at Merritt Island National Wildlife Refuge and in Dixie Co., Florida, and for samples taken 75 km apart in northern Florida (*O. slobodkini* at Tall Timbers Research Station in Leon Co., *O. notulata* near Panacea in Wakulla Co.). No specimens were electrophoretically misclassified with respect to host plant of origin. Multilocus electrophoretic profiles revealed no evidence of hybridization.

*Ophraella slobodkini* is distinguished from *O. communa* not only by morphological but also by electrophoretic characters. Allele frequencies differ strongly at the GPI, IDH1 (slower of two loci), IDH2, anodal malate dehydrogenase (MDH1), cathodal aspartate aminotransferase (AAT2), and LAP loci (Table 2). In Table 2, allele frequencies in a sample of *O. slobodkini* from Tall Timbers Research Station near Iamonia, Fla., are compared with *O. communa* taken from the same fields, and from two localities in Georgia, 29 km and 105 km, respectively, northeast of Iamonia. In these samples, completely diagnostic differences are evident at loci IDH1, IDH2, and MDH1. No evidence of hybridization was observed.

*Discussion.* At all the enzyme loci described above, electromorphs conform to Hardy-Weinberg genotype frequencies within populations both of these and other species of *Ophraella* (Futuyma, 1990; Futuyma and McCafferty, 1990), providing evidence that they are genetic variants. The complete absence of heterozygotes for diagnostic alleles at certain of these loci, even in syntopic or nearly syntopic samples taken from *Ambrosia* and *Iva*, indicates that *O. slobodkini* and *O. notulata* are reproductively isolated sibling species, between which there is little or no gene exchange. Studies in progress by M. C. Keese at Stony Brook indicate that in the laboratory, mating is strongly assortative, and that both adults and hatchling larvae strongly prefer their own host plant in choice tests. These are sister species, sharing synapomorphic states of several morphological characters (the broad eighth sternum of the female, narrow spermathecal receptacle, reduced number of setae on the cardo, extension of the cubital vitta nearly to the apex of the elytron) and electrophoretic characters (Futuyma and McCafferty, 1990). A cladistic analysis of *Ophraella*, based



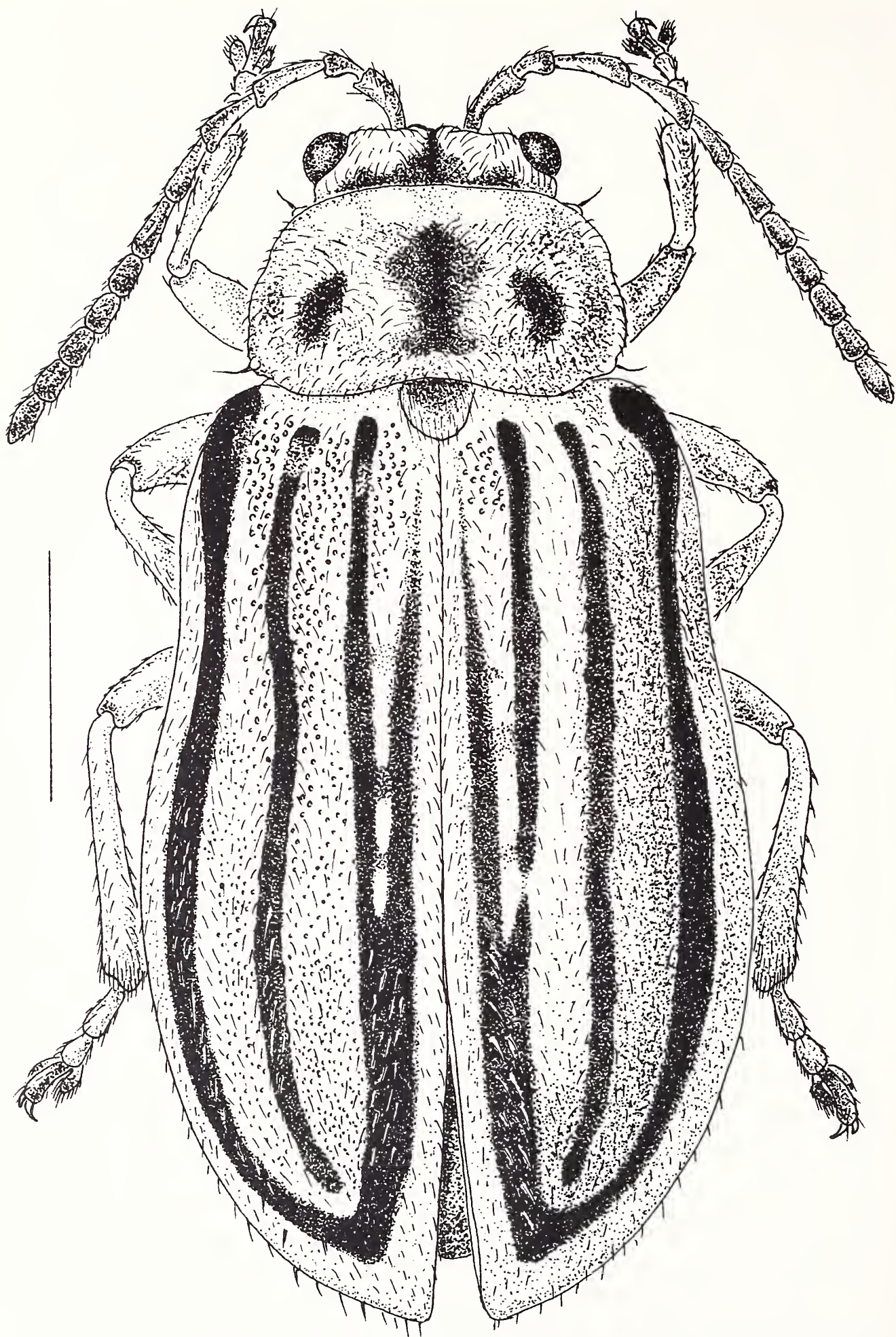


Fig. 1. *Ophraella slobodkini*, female, Slaughter, Withlacoochee National Forest, Pasco Co., Florida, 22 April 1989. Bar = 1 mm.

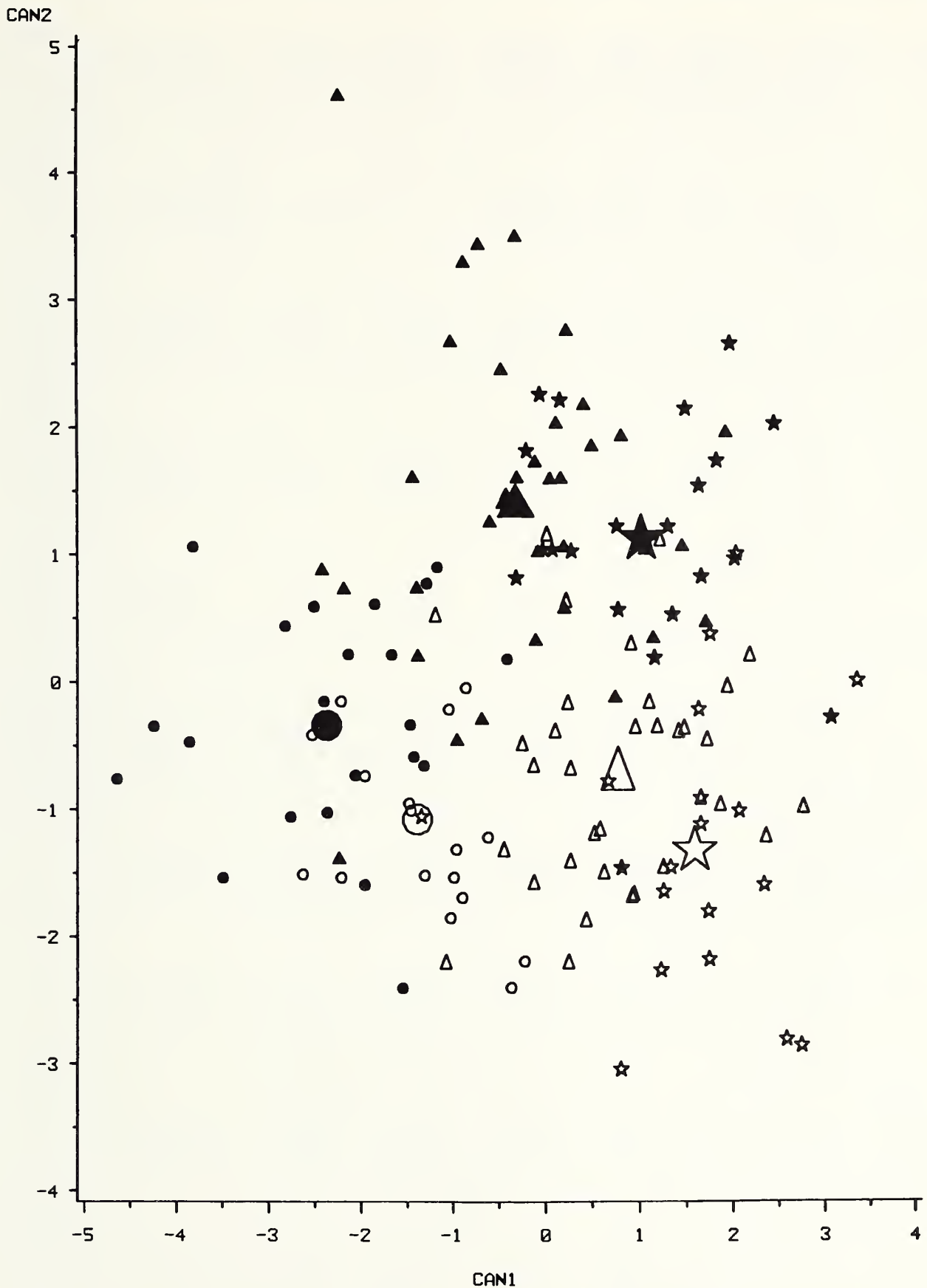


Fig. 2. Canonical discrimination of *Ophraella slobodkini* (triangles), *O. notulata* (stars), and *O. communis* (circles). Open and solid symbols represent individual females and males respectively, and larger symbols represent joint means of the first two canonical variates, which describe two dimensions of shape differences, to each of which several measurements contribute. Axes are marked in unit standard deviations.



Table 2. Allele frequencies at loci showing pronounced frequency differences among *Ophraella slobodkini*, *O. notulata*, and *O. communis*. The first two columns give pooled frequencies for samples of *O. slobodkini* from throughout Florida and for samples of *O. notulata* from localities in Florida and Louisiana. The other columns give frequencies for sympatric or nearly sympatric populations of *O. communis* and *O. slobodkini* (Georgia, Tall Timbers) and of *O. slobodkini* and *O. notulata* (Tall Timbers/Wakulla Co., Merritt Island NWR, Dixie Co.).<sup>1</sup>

Locus allele	<i>O. slobodkini</i> pooled <sup>2</sup>	<i>O. notulata</i> pooled <sup>2</sup>	<i>O. communis</i> Ga.: Tifton, Thomasville	<i>O. communis</i> Tall Timbers, Iamonia, Fla.	<i>O. slobodkini</i> Tall Timbers	<i>O. notulata</i> Wakulla Co., Fla.	<i>O. slobodkini</i> Merritt Is., Fla.	<i>O. notulata</i> Merritt Is., Fla.	<i>O. slobodkini</i> Dixie Co., Fla.	<i>O. notulata</i> Dixie Co., Fla.
GPI	98	81	44	22	33	40	35	30	25	21
4	0.699	0.000	0.011	0.023	0.803	0.000	0.886	0.000	0.940	0.000
5	0.153	1.000	0.932	0.954	0.060	1.000	0.000	1.000	0.000	1.000
IDH1	108	115	44	22	32	54	35	30	25	20
1	0.028	0.000	0.898	0.886	0.000	0.000	0.000	0.000	0.000	0.000
3	0.958	0.996	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH2	88	111	44	21	34	54	35	30	25	20
1	0.006	0.968	0.000	0.000	0.000	1.000	0.000	1.000	0.000	1.000
2	0.000	0.018	0.886	0.809	0.000	0.000	0.000	0.000	0.000	0.000
3	0.989	0.000	0.000	0.000	0.985	0.000	1.000	0.000	1.000	0.000
MDH1	114	90	44	22	34	27	24	23	—	2
1	0.974	0.954	0.000	0.000	1.000	1.000	1.000	1.000	—	0.750
2	0.026	0.006	0.580	0.500	0.000	0.000	0.000	0.000	—	0.000
5	0.000	0.000	0.420	0.500	0.000	0.000	0.000	0.000	—	0.000
AAT2	112	67	44	22	34	27	24	23	—	2
1	0.036	0.000	0.875	0.820	0.000	0.000	0.000	0.000	—	0.000
4	0.964	1.000	0.125	0.180	1.000	1.000	1.000	1.000	—	1.000
LAP	50	74	21	38	33	27	32	30	24	19
3	0.040	0.426	0.000	0.000	0.000	0.555	0.000	1.000	0.000	0.474
5	0.560	0.486	0.000	0.000	0.727	0.333	0.453	0.000	0.479	0.500
6	0.340	0.007	0.690	0.697	0.258	0.037	0.453	0.000	0.521	0.026
8	0.030	0.007	0.286	0.303	0.015	0.000	0.094	0.000	0.000	0.000

<sup>1</sup> Sample sizes are entered above the frequencies at each locus. Allele frequencies may not sum to one because rarer alleles are not listed. For electrophoretic methods and E.C. designations of enzymes, see Futuyma and McCafferty (1990). Relative mobilities of the electromorphs are as follows. The absolute position (in mm) on a typical gel is given in parentheses for the fastest of the designated electromorphs (relative mobility = 1.00). GPI 4 = 1.00 (73), 5 = 0.95. IDH1 3 = 1.00 (16), 1 = 0.81. IDH2 3 = 1.00 (34), 2 = 0.88, 1 = 0.85. MDH1 5 = 1.00 (26), 1 = 0.88, 2 = 0.77. AAT2 1 = 1.00 (-20), 4 = 0.65. LAP 3 = 1.00 (65), 5 = 0.91, 6 = 0.85, 8 = 0.78.

<sup>2</sup> Data are from Futuyma and McCafferty (1990), and do not include all the samples listed in the other columns.



on morphological and electrophoretic data, provided evidence that *O. communa* is the sister group of *O. slobodkini* and *O. notulata* taken together (Futuyma and McCafferty, 1990). Because both *O. communa* and *O. slobodkini* feed on *Ambrosia artemisiifolia*, the most parsimonious interpretation of the evolution of host associations in this group is that the association of *O. notulata* with *Iva frutescens* is derived from an ancestral association with *Ambrosia*.

The known geographic distribution of *O. slobodkini* is much more restricted than that of either *O. notulata* or *O. communa*. The major host of *O. notulata*, *Iva frutescens*, is limited to salt marshes along the Gulf and Atlantic coasts; I have collected this beetle north as far as Long Island, New York, and west as far as Cameron Parish, Louisiana. My only noncoastal record is from Baton Rouge, La., where it was taken on *Iva annua*. Other inland records of *O. notulata* (LeSage, 1986) may represent *O. notulata*, associated with species of *Iva* other than *I. frutescens*, or they may represent *O. slobodkini*; the latter is surely the case for LeSage's records from inland Florida. In peninsular Florida, I have found *O. notulata* on *Iva frutescens* south to Merritt Island on the Atlantic coast and to Crystal River (Citrus Co.) on the Gulf coast. *Ophraella communa* is distributed throughout North America from southern Canada into Mexico, but there are no records from peninsular Florida (LeSage, 1986).

Samples collected from *Ambrosia artemisiifolia*, and conforming to *O. slobodkini* in morphology and allozymes, have been taken from both inland and coastal Florida, from Everglades National Park and Dania in the south to Escambia Co. and Leon Co. (Iamonia) in the north. Eight specimens from Sabine National Wildlife Refuge, Cameron Parish, La., determined electrophoretically as *O. slobodkini*, represent the westernmost record to date. Throughout peninsular Florida, all specimens taken on *Ambrosia artemisiifolia* conform to *O. slobodkini*. This species was found mixed with *O. communa* on *Ambrosia* only in northernmost Florida (*O. slobodkini* comprised 53 of 54 specimens in a collection 19 km west of Pensacola, and about half of a large collection from Tall Timbers Research Station near Iamonia) and in southernmost Georgia (2 *O. slobodkini* and 101 *O. communa* were collected in Thomasville, 29 km northeast of Iamonia). A large collection at Tifton, Ga., 75 km northeast of Thomasville, was composed entirely of *O. communa*, which is also the sole species taken from *Ambrosia* in Athens, Ga., and Baton Rouge, La.

The abruptly complementary distributions of *Ophraella slobodkini* and *O. communa* along the Florida/Georgia border raise the question of whether they are caused by historical or currently acting ecological factors. Many taxa of plants and animals reach their southern or northern range limit in northern Florida, which is also the location of many subspecific boundaries and hybrid zones (Remington, 1968). It has frequently been postulated (e.g., Neill, 1957; Blair, 1965; Remington, 1968) that populations in peninsular Florida differentiated in the Pliocene, when a "Suwannee Strait" may have isolated the region (Frey, 1965), or during the Pleistocene glacial periods, when the biota retreated southward (Deevey, 1949; Auffenberg and Milstead, 1965). Especially during the interglacial periods, a dry corridor along the Gulf coast may have enabled grassland species (including, perhaps, *Ambrosia* and associated insects) to enter Florida from the west (Auffenberg and Milstead, 1965). The palynological record of the late Pleistocene and Holocene indicates that *Ambrosia* and prairie plants were abundant in the dry highlands of central Florida from at least

44,000 years before present (B.P.) until the modern forest began to develop about 4,700 B.P. (Watts, 1980). Along the Florida/Georgia border, a sclerophyllous oak scrub or savanna, probably interspersed with some bluegrass prairie, contained abundant *Ambrosia* from 8,500 to 5,000 B.P., after which a wetter, closed, pine-dominated forest developed, and *Ambrosia* became much less abundant (Watts, 1971, 1980). In the southeastern coastal plain north of Florida, *Ambrosia* pollen is fairly abundant from 29,000 to 9,500 B.P., after which it is much less common (Watts, 1980). *Ambrosia*, possibly harboring populations of *Ophraella*, has therefore long been resident throughout the region. Thus, although latitudinal shifts in vegetation during the several glacial maxima may have provided opportunity for peninsular Floridian populations to become differentiated, *Ambrosia* and associated insects may have been fairly continuously distributed from peninsular Florida to the mainland throughout the late Quaternary, except perhaps in the last several thousand years.

For many reasons, estimates of divergence time based on genetic distances between species (Nei, 1987) are subject to considerable error (Futuyma and McCafferty, 1990). Nevertheless, if we apply Nei's (1987) suggested calibration, the genetic distance between *Ophraella slobodkini* and *O. notulata* (Nei's  $D \sim 0.21$ ) implies divergence about 1.1 million years ago, and that between *O. slobodkini* and *O. communa* ( $D \sim 0.35$ ) about 1.7 million years, i.e., in the early to mid-Pleistocene. There is no direct evidence that *O. slobodkini* differentiated from *O. communa* in peninsular Florida; but even if it did so, there has been ample opportunity, given the historical distribution of *Ambrosia*, for *O. slobodkini* and *O. communa* to penetrate each other's range, unless *O. communa* has spread very recently to eastern North America from the west (its likely region of origin, because the closest relatives of the *O. communa*-*O. slobodkini*-*O. notulata* clade have more western distributions: Futuyma and McCafferty, 1990). The considerable uniformity of allele frequencies among populations of *O. communa* and of *O. slobodkini* implies substantial gene flow and vagility. They feed on a plant that at least currently is abundantly distributed across the region of replacement, and which, being an early-successional annual, is often only briefly available in a given site, so that dispersal of the beetles is forced. It is likely that human activities provided openings in which *Ambrosia* could thrive for many centuries before the European settlement (Remington, 1968). Thus current ecological factors are probably responsible for the sharply complementary distributions of these species. Throughout its broad range, *O. communa* occupies its host plant in habitats ranging from mesic to almost xeric; it does not appear highly sensitive to edaphic conditions. This suggests that biological interactions might influence the distributions of these species. In view of the common supposition that competition for resources is rare in folivorous insects (Slobodkin et al., 1967; Schoener, 1983; Connell, 1983; Price, 1983; Strong et al., 1984; but see Faeth, 1988), the possibility that these species' distributions are caused by competitive exclusion is intriguing.

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## LITERATURE CITED

- Auffenberg, W. and W. W. Milstead. 1965. Reptiles in the Quaternary of North America. Pages 557–568 *in*: H. E. Wright, Jr. and D. G. Frey (eds.), *The Quaternary of the United States*. Princeton University Press, Princeton, N.J.
- Blair, W. F. 1965. Amphibian speciation. Pages 543–556 *in*: H. E. Wright, Jr. and D. G. Frey (eds.), *The Quaternary of the United States*. Princeton University Press, Princeton, N.J.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Amer. Natur.* 122:661–696.
- Deevey, E. S. 1949. Biogeography of the Pleistocene. *Geol. Soc. Amer. Bull.* 60:1316–1416.
- Faeth, S. H. 1988. Plant-mediated interactions between seasonal herbivores: enough for evolution or coevolution? Pages 391–414 *in*: K. C. Spencer (ed.), *Chemical Mediation of Coevolution*. Academic Press, London.
- Frey, D. G. 1965. Other invertebrates—an essay in biogeography. Pages 613–631 *in* H. E. Wright, Jr. and D. G. Frey (eds.), *The Quaternary of the United States*. Princeton University Press, Princeton, N.J.
- Futuyma, D. J. 1990. Observations on the taxonomy and natural history of *Ophraella* Wilcox (Coleoptera: Chrysomelidae), with a description of a new species. *J. N. Y. Entomol. Soc.* 98:163–186.
- Futuyma, D. J. and S. S. McCafferty. 1990. Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera: Chrysomelidae). *Evolution* 44: 1885–1913.
- LeSage, L. 1986. A taxonomic monograph of the Nearctic galerucine genus *Ophraella* Wilcox (Coleoptera: Chrysomelidae). *Mem. Entomol. Soc. Canada* No. 133:1–75. Ottawa, Ont.
- Menken, S. B. J. 1989. Electrophoretic studies on geographic populations, host races, and sibling species of insect pests. Pages 181–202 *in*: H. D. Loxdale and J. den Hollander (eds.), *Electrophoretic Studies on Agricultural Pests*. Systematics Association Special Volume No. 39, Clarendon Press, Oxford.
- Nei, M. 1987. *Molecular Evolutionary Genetics*. Columbia University Press, N.Y.
- Neill, W. T. 1957. Historical biogeography of present day Florida. *Florida State Mus. Bull. Biol. Sci.* 2:175–220.
- Price, P. W. 1983. Hypotheses on organization and evolution in herbivore communities. Pages 559–596 *in*: R. F. Denno and M. S. McClure (eds.), *Variable Plants and Herbivores in Natural and Managed Systems*. Academic Press, New York.
- Remington, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. *In*: Th. Dobzhansky, M. K. Hecht and W. C. Steere (eds.), *Evolutionary Biology* 2:321–428. Appleton-Century-Crofts, N.Y.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *Amer. Natur.* 122: 240–285.
- Slobodkin, L. B., F. E. Smith and N. G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. *Amer. Natur.* 101:104–124.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. Freeman, San Francisco.
- Strong, D. R., Jr., J. H. Lawton and R. Southwood. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell, Oxford.
- Watts, W. A. 1971. Postglacial and interglacial vegetation history of southern Georgia and central Florida. *Ecology* 52:676–690.
- Watts, W. A. 1980. The Late Quaternary vegetation history of the southeastern United States. *Annu. Rev. Ecol. Syst.* 11:387–409.
- Wilcox, J. A. 1965. A synopsis of North American Galerucinae (Coleoptera: Chrysomelidae). *Bull. N.Y. State Mus. Sci. Serv.* 400:1–226.

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